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Acarospora scottii and *Sarcogyne paradoxa* spp. nov. from North America

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Abstract—*Acarospora scottii,* a facultative lichenicolous lichen on crustose lichens, is described and typified from Minnesota. *Sarcogyne paradoxa,* which is described and typified from California, grows as an endolithic lichen or as a lichenicolous fungus endokapylic in crustose lichens.

Key words—*Acarospora americana*, *Acarosporaceae*, New Mexico, *Polysporina,* taxonomy

Introduction

Lichenicolous lichens begin their life cycle as non-lichenized parasites in the microbiomes of lichens, expropriate the algae of the host, and eventually morph out of the host thallus, destroying the host (Diederich & al. 2018; Knudsen & Kocourková 2018a; Knudsen & al. 2012, 2014). They persist as lichenized fungi in a new epilithic thallus that differs from the host form. Two hundred fifty-eight obligatory and facultative species have been reported worldwide (Diederich & al. 2018, Knudsen & Kocourková 2018a). Reports in older literature are not based on this distinction and may not be parasites but crustose lichens that overgrow and destroy other lichens in the competition for space (although winning the competition may bestow a saprobic benefit).

Obligatory lichenicolous lichens always begin their life cycle as juvenile non-lichenized parasites. Obligatory lichenicolous lichens can be host specific. For instance, *Heteroplacidium transmutans* K. Knudsen & al. from

the Sonoran Desert has only been found growing out of *Acarospora socialis* H. Magn. and has only been found as an independent lichen in association with populations of its host (Knudsen & al. 2014). Or obligate lichenicolous lichens can be opportunistic, occurring on different species or genera. For instance, *Diploschistes muscorum* (Scop.) R. Sant. parasitizes many different *Cladonia* species and (rarely) is parasitic on *Lepraria xerophila* Tønsberg and *Leprocaulon americana* Lendemer & B.P. Hodk. in coastal habitats in southern California (Kocourková & al. 2012).

Facultative lichenicolous lichens can begin as a non-lichenized parasite in the microbiome of a lichen, although they usually begin their life cycle as non-parasitic lichenized fungi. They are also usually opportunistic, although records may be based on only one host. A classic example of a facultative lichenicolous lichen is *Acarospora succedens* H. Magn. It was described from a single specimen as a parasite on *Dimelaena suboreina* (B. de Lesd.) Hale & W.L. Culb. in New Mexico (Magnusson 1930). The taxon was described again from New Mexico as the non-parasitic lichen *A. interspersa* H. Magn., which is frequent in the Chihuahuan and Sonoran Deserts and is rarely found as a parasite on crustose lichens (Knudsen 2007, 2011; Magnusson 1933). In this paper we describe a facultative lichenicolous lichen, *Acarospora scottii,* from Minnesota and Ontario, Canada.

In contrast to lichenicolous lichens, we describe *Sarcogyne paradoxa* which occurs as either a non-lichenized parasite dwelling in the microbiome of crustose lichens or as an endolithic lichen. It grows in the Mojave Desert and other xerothermic habitats in Asia and North America. The implications of *S. paradoxa* for a revision of species of the polyphyletic genus *Polysporina* is discussed.

Material & methods

A specimen collected by Perry Scott, a citizen lichenologist, and specimens from ASU & UCR herbaria were studied using standard microscopy and spot tests. The amyloid reaction of the hymenial gel and subhymenium was tested with fresh undiluted IKI (Merck's Lugol; see protocol in Knudsen & Kocourková 2018b). Measurements were made in water. Macrophotographs were taken with the Olympus DP74 digital camera mounted on Olympus SZX 16 stereomicroscope equipped with PRO-SZM1 - Focus Drive Motorization for stacking pictures and stacked using Olympus DeepFocus 3.4 module of Promicra QuickPhoto Camera 3.2 software. The figure plates were processed with the same software fitted with Promicra Figure Maker modul and eventually refined with Adobe Photoshop CS4 Extended ver. 11.0.

Taxonomy

Acarospora scottii K. Knudsen & Kocourk., **sp. nov.** Figs 1, 2

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Similar to *Acarospora americana* but differing in having dark blue hymenial gel in Lugol's (euamyloid), in having a continuous polysaccharide epicortex giving the areoles a dark shiny appearance, and in having a cortex of vertical hyphae.

Type: USA, Minnesota, Cook. Co., Superior National Forest, Caribou Rock Trail, on vertical east-facing side of Caribou Rock, 48.06380°N 90.45655°W, 560 m, on unknown crustose lichen and *Aspicilia* species and independent on diabase, 6 August 2017, P.A. Scott 5416 (**Holotype**, PRM!)

Etymology: Named in honour of the collector, citizen lichenologist Perry Scott, who collected the new species.

Hypothallus endolithic, continuous with medulla, no algae observed, broadly and firmly attached or becoming loosely attached and squamulose, replicating by division. Thallus of areoles ≤1.3 mm wide, round to angular, flat to bullate, 300–500 µm thick, broadly attached, replicating by division. Upper surface dark brown, shiny, epruinose, black edged. Lower surface usually dark brown. Epicortex 5 µm thick, continuous. Cortex 30–50 µm thick, of distinct vertical hyphae, 2–3 µm wide, breaking up into irregular cells, terminating in expanded apices, 4–5 µm wide in dark brown gel cap, upper layer of cortex dark brown, c. 10 µm high, lower layer hyaline. Algal layer continuous without hyphal bundles, 50–100 µm thick, algal cells 10–15 µm wide. Medulla 150–300 µm thick, hyphae thin-walled, 2–3 µm diam.

Apothecia usually 1 per areole, rarely 2 to 6, immersed ≤1 mm wide, the disc epruinose, rugulose, usually round. Parathecium indistinct or narrow to 15 µm wide, intergrading with cortex. Epihymenium 10–20 µm thick, coherent, brown to yellowish brown, sealed with polysaccharide hyaline layer c. 5 µm, a continuation of the epicortex. Hymenium (including epihymenium) 100–120(–150) µm tall, highest in bullate areole, hymenial gel IKI+ blue (euamyloid). Paraphyses 1.5–2 µm diam. at mid-level, apices expanded to 3 µm in pigment cap with blackish pigment mark, often with abundant oil drops. Asci 70–90 × (8–)10–12(–15) µm, narrow, c. 100 ascospores per ascus. Ascospores 3–4(–5) × 1.5–2 µm. Subhymenium 30–50 µm thick, IKI+ blue (euamyloid). Hypothecium 10 um wide. Pycnidia not observed. Spot tests negative, K–, KC–, C–, P–.

Selected additional specimens examined: **CANADA. Ontario.** Thunder Bay District, Sleeping Giant Provincial Park, by shore of Lake Superior, 48.31463°N 88.88739°W, 190 m, on diabase bedrock and on Aspicilia species, 7 September 2019,

P.A. Scott 7030 & J. Hollinger (hb. Scott). **USA. Minnesota**, **Cook Co.**, Boundary Waters Canoe Area Wilderness, near west end of Mountain Lake, 48.09710°N, 90.28500°W, 595 m, on *Aspicilia* species on northwest facing diabase rocks near top of cliff, 15 August, 2019, P.A. Scott 6837 (hb. Scott), Superior National Forest, southwest-facing cliff overlooking Moss Lake, 48.0654°N 90.4611°W, on diabase, 5 August 2017, P.A. Scott 5405A (hb. Scott), Caribou Rock, Caribou Rock Trail, on exposed vertical east-facing rock near top of cliff, 48.06380°N, 90.45640°W, 560 m, on Aspicilia species and on diabase, 11 August 2019, P.A. Scott 6767 (NY), 6768 (hb. Scott).

Ecology & distribution. Epilithic on diabase and/or parasitic on crustose lichens in North America. Diabase sills form the caps of the cliffs in this area of Minnesota. Expected to be more widespread in United States and Canada on other intermediate siliceous rocks poor in SiO_2, possibly also on more acid rock. Specimens in herbaria are probably identified as *A. americana* H. Magn. or *A. veronensis* A. Massal.

Discussion. *Acarospora scottii* is similar to *A. americana* but differs in having areoles that are not dull brown but shiny due to a continuous polysaccharide epicortex and in having a consistent black margin around the edge of areole and becoming squamulose with dark brown to black lower surface. It also differs in having euamyloid hymenial gel in Lugol's vs. hemiamyloid hymenial gel in Lugol's and in having a cortex of vertical or irregular hyphae vs. distinctly paraplectenchymatous hyphae (Knudsen & al. 2011). *Acarospora americana* has a parathecium that usually widens around the apothecial disc, even forming an elevated parathecial crown the same color as thallus. *Acarospora scottii* has an indistinct or narrow parathecium, often intergrading with the cortex, but in some specimens may have a raised thalline collar surrounding and higher than the apothecial disc.

Acarospora veronensis differs from *A. scottii* in having a narrow cortex (c. 15 µm vs. 30–50 µm thick) and in having hemiamyloid hymenial gel in Lugol's.

Acarospora scottii is a typical facultative lichenicolous lichen. Its non-lichenized hypothallus spreads through the upper layer of the rock. In patches of bare rock, the hypothallus parasitizes algae forming an epilithic lichen thallus. Spreading under crustose lichens, the hypothallus penetrates them from below, expropriating the algal photobiont from the host, eventually destroying the mycobiont. It morphs out of the host forming an epilithic lichen thallus. In *A. scottii*, the areoles that emerged from crustose lichens are much more robust, thicker or bullate than the areoles growing on bare rock (Figs 1, 2). This suggests that not only are they receiving nutrition from the photobiont of the host but also from the saprobic absorption of the

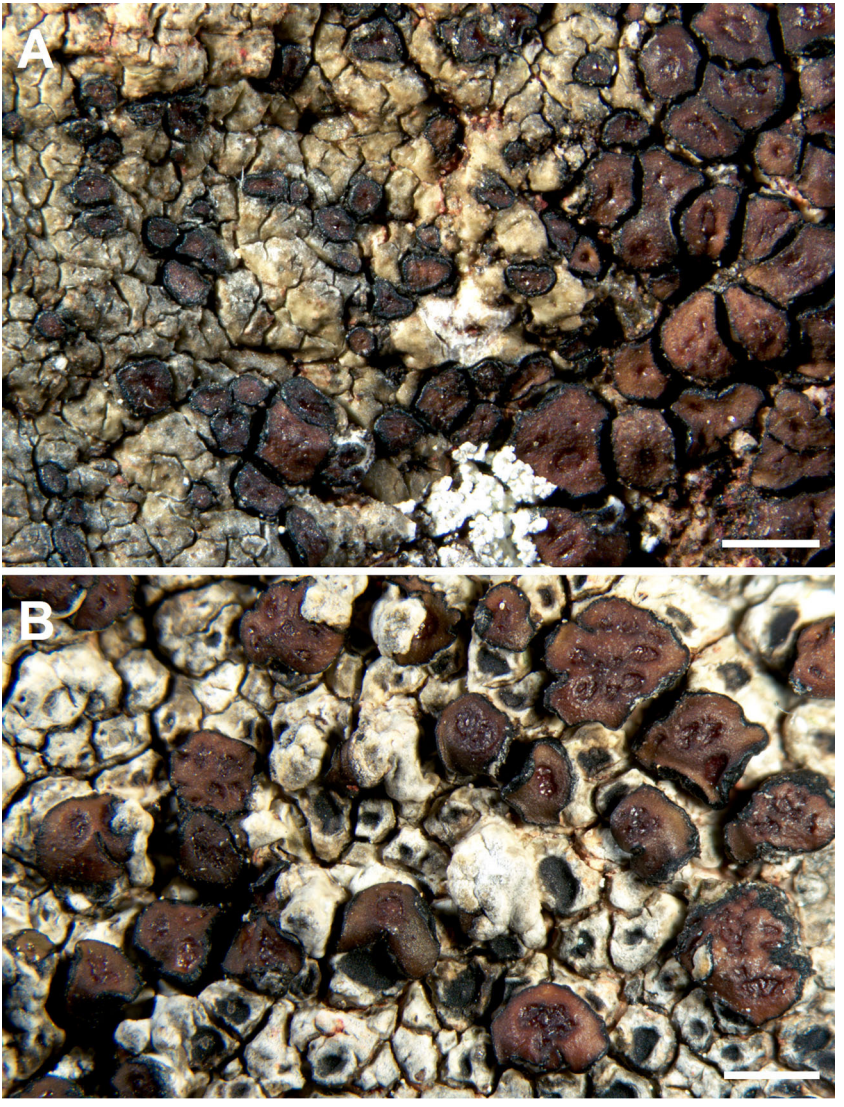

Fig. 1. *Acarospora scottii* (holotype, PRM – Scott 5416). A. Areoles emerging from unknown crustose lichen; B. Thick or bullate areoles emerging from *Aspicilia* thallus. Scale bars = 1 mm.

mycobiont of the host. Such a difference is not distinctive in other facultative lichenicolous lichens we have studied, for instance *A. schleicheri* (Ach.) A. Massal. Like most facultative lichenicolous lichens it is opportunistic and

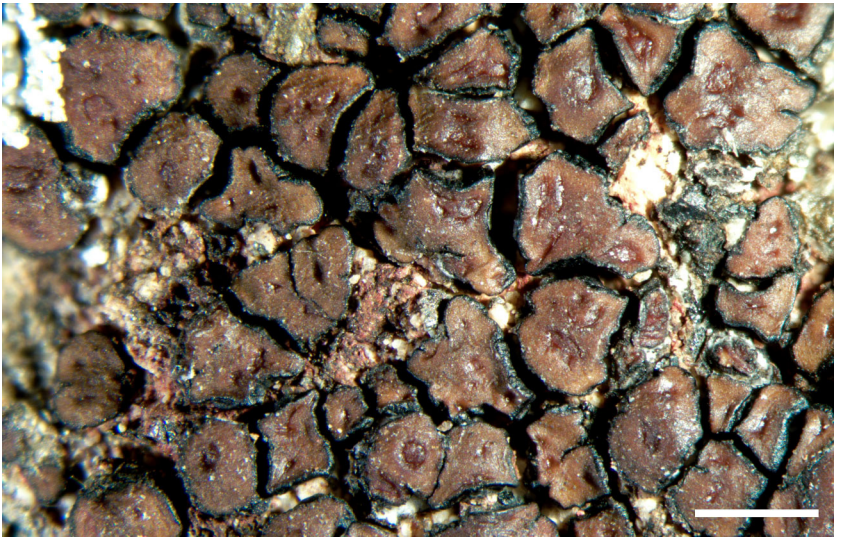

Fig. 2 *Acarospora scottii* (holotype, PRM – Scott 5416).
Areolate thallus with flat areoles growing on bare rock. Scale bar = 1 mm.

not host specific (in holotype it occurs on *Aspicilia* species and unknown crustose lichen). The paratype was non-lichenicolous.

Areoles in the holotype were often sterile or with only a few mature asci. The holotype was collected during summer in Minnesota, suggesting ascospores are released seasonally, possibly early spring, at least in Minnesota.

Sarcogyne paradoxa Kocourk. & K. Knudsen, **sp. nov.** Fig. 3

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Differs from *Acarospora subfuscescens* by its reddish brown to brown apothecia that remain brown when hydrated.

Type: USA, California, San Bernardino Co., Joshua Tree National Park, below Belle Mountain, in unnamed wash, 34.0189°N 116.0025°W, 1382 m, common on granite boulder on wash, apothecia emerging from rock, 22 August 2005, K. Knudsen 3620 (**Holotype**, UCR; **isotype**, ASU).

Etymology: Named because it grows as either an endolithic lichen or a lichenicolous fungus.

Thallus in non-parasitic specimens endolithic, the algal layer occurring in the substrate below the apothecia beneath a mycelial base continuous with hypothecium. In parasitic specimens endokapylic, no algal layer occurring in substrate below host, apothecia emerging from the host.

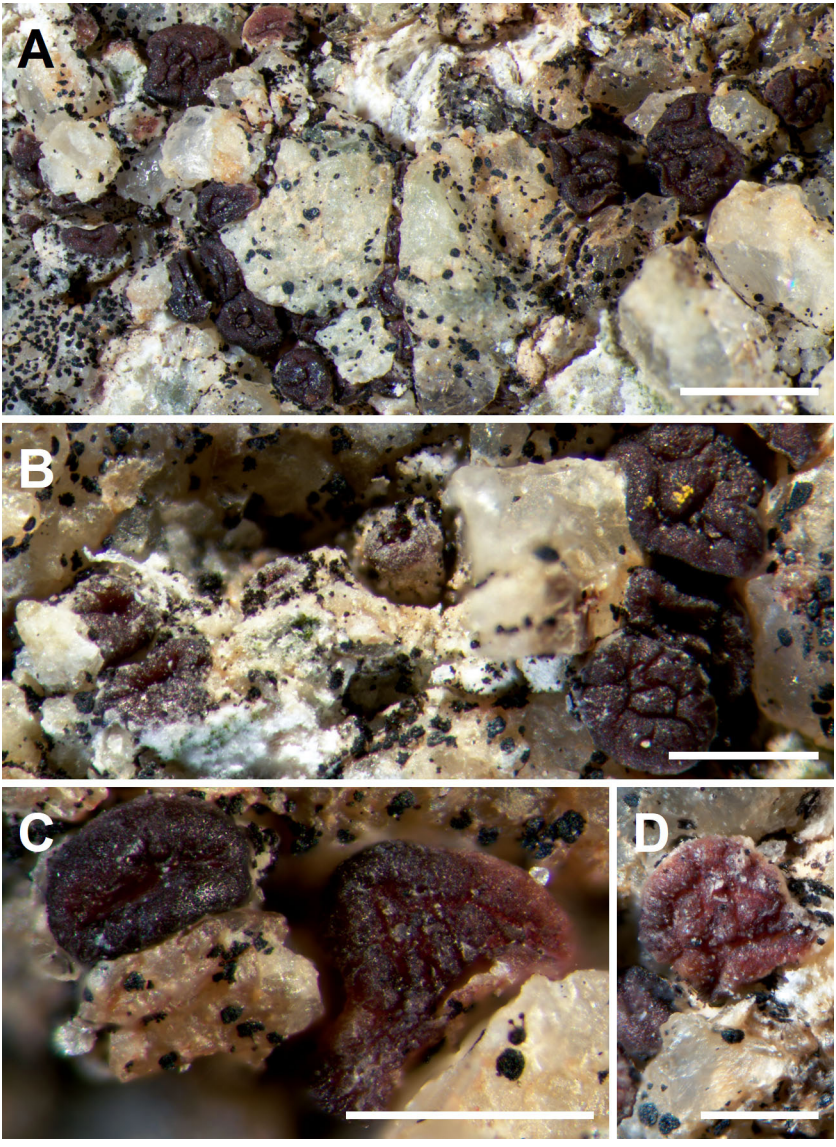

Fig. 3 *Sarcogyne paradoxa* (holotype, UCR – Knudsen 3620). A. Habit of the thallus in rock crevices (with *Lichenothelia* species); B. Emerging and developed apothecia; C. Apothecia with conspicuous elevated margins; D. Fully developed apothecium with rugose surface. Scale bars: A = 1 mm; B, C = 500 µm; D = 200 µm.

Apothecia superficial on host or occurring on substrate, brown when dry or wet, 0.5–1.0 mm diam, round or irregular, dispersed or contiguous, forming clusters of apothecia to 3 mm wide; disc brown to reddish brown, convex, with furrows, ridges, and umbos, rough and uneven, margin distinct but becoming fissured. Parathecium to 100 µm wide, hyphae mostly 2–3 µm diam, septate, cells mostly 2–3 µm wide, ending in expanded apices forming outer wall of the margin. Outer layer of margin reddish-brown to dull brown, 20–30 µm thick; inner layer hyaline. Epihymenium 10–20 µm thick, in reddish brown gel, accretions on surface of disc to 200 µm high formed from the epihymenial gel. Hymenium 80–120 µm tall, hyaline, hymenial gel IKI+ deep blue (euamyloid), paraphyses coherent (1–)2–3 µm diam, sometimes constricted at septa, infrequently branching in lower half, unexpanded or expanded apices sometimes in darker pigment caps. Asci 60–90 × 12–20 µm, ascospores mostly 100 per ascus, ascospores (3.0–)4.0–4.5(–7) × 2.0–3.0 µm, mostly broadly ellipsoid. Subhymenium hyaline, 30–50 µm thick, IKI+ blue. Hypothecium up to 50 µm thick, continuous with vegetative vertical hyphae forming a mycelial base above algal layer in substrate. Pycnidia not seen. Spot tests C–, KC–, K–. P–.

Selected additional specimens examined: **California**, **San Bernardino Co.**, Granite Mountains: Sweeney Granite Mountains UC Reserve, Sibyl Allison trail, 34.7892°N 115.6717°W, 1692 m, on granite, 14 December 2007, K Knudsen 8050 & R. Muertter (UCR). **Santa Barbara Co.**, Channel Island National Park, Santa Rosa Island, south slope of South Peak, 33.9064°N 120.1283°W, 243 m, on unknown host and independent on sandstone, 15 August 2007, K. Knudsen 8762.2 (UCR). **San Luis Obispo Co.**, San Simeon, San Simeon State Park, Molinari Property, exposed slab of volcanic rock next to ravine along old Highway One dirt road, 35.6039°N 121.1275°W, 41 m, on crustose lichen, 8 January 2007, K. Knudsen 8116 (UCR)

Ecology & distribution. Occurring in siliceous rock, usually granite, as an endolithic lichen or endokapylic in the thallus of crustose lichens as a non-lichenized parasite in North America (California) and Asia (Afghanistan, Xinjiang in China) (Knudsen & Kocourková 2008, 2009; L. Nurtai, pers comm.) The specimen from Afghanistan at GZU is a parasite on an unknown lichen on granite. The specimens from Xinjiang are endolithic lichens on granite. Based on the distribution of *Acarospora gyrocarpa* (H. Magn.) K. Knudsen & M. Westb. [≡ *Polysporina gyrocarpa* (H. Magn.) N.S. Golubk.] in China and southwestern United States, *S. paradoxa* is expected like *A. gyrocarpa* to be widespread but probably rare in the Chihuahuan, Mojave, and Sonoran Deserts in southwestern North America. (Knudsen & Kocourková 2009). The species is easily over-looked in field inventories.

Discussion. *Sarcogyne paradoxa* differs from the lichenicolous fungus *Acarospora subfuscescens* (Nyl.) H. Magn. in having brown apothecia with epihymenial accretions that are brown when hydrated instead of dark brownish black to black apothecia with epihymenial accretions that are black when hydrated (Knudsen & Kocourková 2008). *Sarcogyne paradoxa* was treated previously as *Polysporina arenacea* (H. Magn.) K. Knudsen & Kocourk. [a misapplication] and was only subsequently recognized as a lichenicolous fungus (Knudsen & Kocourková 2008). *Acarospora arenacea* H. Magn. is a rare lichen known only from Utah and North Dakota, USA (Magnusson 1952). In phylogenetic analyses *S. paradoxa* falls into the *Sarcogyne* lineage (Westberg & al. 2015, Knudsen & al. 2019).

Sarcogyne paradoxa has a different lifestyle from lichenicolous lichens like the obligatory *Diploschistes muscorum* or the facultative *Acarospora scottii.* It can be a lichen; the hyphae of the hypothallus parasitizes algae occurring in rock in the upper 1 mm of the substrate, forming an endolithic lichenized thallus that eventually produces epilithic apothecia. Or it can be a lichenicolous fungus, the endolithic hypothallus apparently entering the host from beneath the thallus. It does not expropriate the algae of the host like a lichenicolous lichen, eventually forming an independent epilithic thallus. Like many lichenicolous fungi, it expropriates a portion of the carbon produced by the photobiont of the lichen host but maintains a symbiotic relationship, not destroying the host. In the few specimens seen, it does appear to suppress the host forming apothecia, which would conserve for its nutrition carbon produced by the photobiont of the host that would otherwise nourish the sexual reproduction of the host.

During our work on the genus *Polysporina* Vězda, we used broad morphological and anatomical species concept of *Polysporina subfuscescens* (Nyl.) Knudsen & Kocourk. for identifying taxa growing on lichens and a broad concept of *Polysporina simplex* (Borrer ex Hooker) Vězda for identifying lichenized taxa growing on rock (Knudsen & Kocourková 2008; Westberg & al. 2015). Based on phylogenetic analyses of a large sampling of specimens, *Polysporina* was found to be polyphyletic with most taxa occurring in several different lineages of *Acarospora* (Westberg & al. 2015). In that tree, the lineages *Polysporina* A and *Polysporina* B contained specimens identified as *P. subfuscescens* (lichenicolous fungus) and *P. simplex* (endolithic lichen). These two lineages apparently represent single species, both of which either occur as a lichenicolous fungus or an endolithic lichen like *Sarcogyne paradoxa*. Because *Polysporina* is polyphyletic and negated as

a monophyletic genus, we treat the taxa as *Acarospora* or *Sarcogyne* based on their position in the current phylogenetic trees of *Acarosporales* (Westberg & al. 2015; Knudsen & al. 2019). *Acarospora subfuscescens* and *Acarospora simplex* (Borrer ex Hooker) Jatta are heterogeneous in these phylogenetic analyses and obviously in need of a revision (Gueidan & al. 2014, Westberg & al. 2015).

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